IMPACT OF TEMPERATURE ON COLONY GROWTH AND DEVELOPMENTAL RATES OF THE ANT, *SOLENOPSIS INVICTA*

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Abstract—Growth rates of the fire ant, *Solenopsis invicta*, were studied across a range of constant temperatures. Growth in established colonies only occurred at rather warm temperatures: between 24 and 36°C, with maximal growth around 32°C. Colony growth ceased below 24°C even though 17°C was the theoretical minimum for brood development. Total developmental time (egg to adult) for minor worker brood decreased from 55 days at 24°C to 23 days at 35°C. The proportion of time required by each developmental stage (i.e. eggs, larvae, pupae) was independent of temperature. Nanitic brood developed about 35% faster than did minor worker brood, an important benefit for founding colonies. Data are still fragmentary, but it appears that temperature-adjusted development rates of ants and other social Hymenoptera are quite similar.

Key Word Index: Temperature, colony growth, developmental rates, fire ant, *Solenopsis invicta*, social Hymenoptera

INTRODUCTION

Changing environmental temperatures strongly affect the growth of brood in ant colonies (Wheeler, 1910); however, quantitative measures of thermal effects are scarce (Brian, 1963; Markin *et al.*, 1972; Passera, 1974; Elmes and Wardlaw, 1983). Approximate developmental times have been reported for a number of ants under laboratory or field conditions (e.g. Curtis, 1985; MacKay, 1981; Mintzer, 1979; Schneirla, 1971; Talbot, 1943; Weber, 1972), but precise developmental times at particular temperatures are only available for a few species (Peacock and Baxter, 1950; O'Neal and Markin, 1975a; Wheeler, 1982; Newell, 1909). The purpose of this study was to examine how temperature affects rates of brood development and overall colony growth in the fire ant, *Solenopsis invicta*.

MATERIALS AND METHODS

Investigations were conducted in Tallahassee, Florida (1984–1986) with monogyne fire ant populations. Collecting, handling, and feeding procedures were similar to those described by Banks *et al.* (1981). Colonies were kept in environmental chambers at one of seven experimental temperatures (°C ± SD): 17 ± 1.5, 21 ± 0.5, 24.5 ± 0.5, 28.5 ± 0.3, 30 ± 0.1, 32 ± 0.1 and 35 ± 0.1. Fans were used to provide a more uniform temperature distribution in the chambers. Probes were also placed near the nests to measure temperatures actually experienced by the colonies. Colony fragments used in brood development investigations were kept in test tube nests (13 by 100 mm) that had been partially filled with water and plugged halfway with a cotton ball. Tubes used for egg development tests and claustrally founding queens were plugged at the end with a second cotton ball. Tubes used for larval and pupal development tests were placed in foraging trays and capped with a small piece of aluminium foil in which an exit hole had been punched.

The duration of the egg stage was determined from short-term pulses of eggs laid by four physogastric queens maintained at 28°C. Eggs were collected by isolating these queens with a few of their workers for 6–10 h. At the end of this period, the resulting egg mass from each queen was removed and divided into seven equal clusters of eggs (25–100, depending on how many were laid). These clusters were placed with separate founding queens which immediately adopted the test eggs and began tending them. These founding queens had been stored at 17°C for 2 months; this storage substantially reduced the number of eggs they were able to lay. The few eggs which the founding queens did lay could be discriminated because of their large size (Tschinkel, 1988a). A total of four replicate sets of eggs were set up at each of the seven experimental temperatures. Two differences existed between replicates: Eggs used in the first replicate were dyed by feeding Rhodamine B to the colony a week or so before collecting the queen's eggs. Dyeing test eggs was discontinued in subsequent replicates after confirming there was no danger of confusing test eggs with those laid by the founding queens. The other difference was that three small workers were substituted for the founding queen in the fourth replicate. Eggs in all four replicate sets were inspected daily under a dissecting microscope (see Petralia and Vinson, 1979) to determine time of hatch.

In order to determine the duration of the larval stage, eggs were collected from established physogastric queens as described above. These eggs were divided into clusters of about 100 eggs and then incubated at 28°C with a few workers until they began to hatch. At this point, clusters were transferred into groups of 50 workers and 50 late instar larvae. Late-instar larvae had been dyed blue by

feeding them Nile Blue A; this was done to avoid confusing them with the growing test larvae. Late-instar larvae were included in test units because informal observations suggested they promoted the growth of the early instar larvae. Colony fragments were fed and inspected for larval development daily. Six replicate groups were established at each temperature (except 17°C) using workers and larvae from a new source colony for each set.

The duration of the pupal stage was determined by placing ten worker prepupae collected from field colonies into nests with 6–10 workers. Eight replicate sets were used with one nest from each set at each experimental temperature. Three additional replicate sets were established using sexual prepupae. Nests were checked daily to determine what percentage of brood had died, pupated, or eclosed into callow workers. The duration of the pupal stage was estimated by comparing the time for 50% pupation with that for 50% eclosure. Developmental times of pre-pupae and pigmented pupae were also determined in a similar manner using three and five replicates, respectively. Prepupae (pharate pupae) are non-feeding larvae that have voided their guts and turned opaque white in preparation for pupation. Pigmented pupae are those in which the head and body have turned yellow prior to eclosure of the adult. These developmental substages were included because they are fairly distinct categories which will be used to provide short-term estimates of colony growth in a future paper.

The effect of temperature on development of nanitic (miniature) workers produced in founding colonies was studied by collecting about 270 newly mated queens from three mating flights (May, June, October). Between 12 and 15 queens from each flight were individually established in sealed test tube nests at each experimental temperature. Developmental stages in these colonies were recorded every day or two. Queens producing infertile eggs or diploid males were eliminated from experimental analyses (Porter and Tschinkel, 1986).

The effect of temperature on colony growth was investigated with two sizes of queenright colonies. Large colonies started with 1.0 g of workers (~2000) and 0.5 g of brood (~1000). Small colonies contained about three dozen nanitic workers and were established immediately after the claustral founding period. Both sizes were fed excess quantities of crickets and 1 M sugar-water daily. Colony growth was determined after 1 and 2 months by counting and weighing the workers, larvae and pupae produced.

RESULTS

Development

Temperature substantially affected brood development in the fire ant, *S. invicta*. Developmental rates for brood in established and founding colonies are presented separately.

Brood from established colonies. The duration of the egg stage decreased from 11 days to 5 days as temperature increased (Fig. 1). Eggs at 17 and 20°C failed to develop and disappeared in the first week, apparently eaten by the queen or workers.
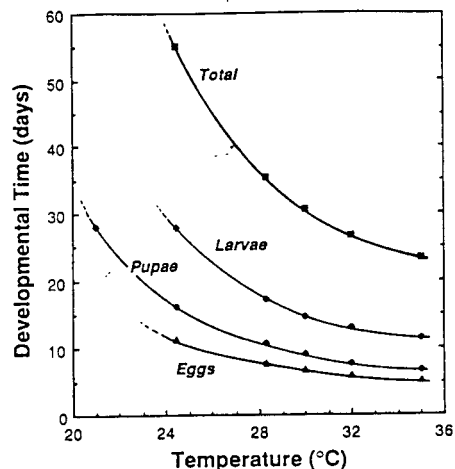

Fig. 1. Effect of temperature on developmental times of minor worker brood in the fire ant, *Solenopsis invicta*. Means for larvae and pupae are from 4 replicates; pupae are from 8 replicates. Standard errors were too small to show (±0.1–0.6).

The duration of the larval stage declined from 28 days to 11 days as temperature increased (Fig. 1). Data for larvae are based on four replicate sets because young larvae did not develop in two of the original six replicates. About 20% of larvae introduced into successful test colonies eventually pupated. Low survival is probably related to the large number of larvae initially introduced and the small size of the experimental colonies. Also, young larvae may have cannibalized some of the unhatched test eggs. The lack of a colony queen could have been another factor. Larvae which pupated in these test units eclosed into minor workers similar in size to those normally produced in small- or medium-sized laboratory colonies. Minor workers (head width: 0.7 ± 0.1 mm) comprise about 75% of workers in mature colonies (Porter and Tschinkel, 1985a) and almost all workers in young colonies (Tschinkel, 1988b).

The duration of the pupal stage declined from 28 days at 21°C to less than 7 days at 35°C (Fig. 1). In contrast to eggs and larvae, pupae were able to complete development at temperatures as low as 21°C. Some development was even observed at 17°C—prepupae eventually eclosed into pupae, but these pupae invariably died before adult workers emerged. Survival of pupae to eclosure averaged 79–86% ($\bar{x} = 84 \pm 3\%$, SD) at temperatures from 21–35°C. Survivorship within this range was not related to temperature (two-way ANOVA blocked for trials, $F = 1.38$, d.f. = 5,20, $P > 0.05$).

Total developmental time (Fig. 1) was calculated by adding developmental times for eggs, larvae and pupae. These totals declined from 55 days at 24.5°C to 23 days at 35°C (Fig. 1). These values are very close to those observed by other investigators. O'Neal and Markin (1975a) reported a developmental time of 24 days for minor *S. invicta* workers at 32°C; this compares to 26.7 days reported here (Fig. 1). Diana Wheeler (person. commun.) observed total development times of 29–31 days at 30°C which matches my estimate of 30.5 days (Fig. 1). According to Wheeler,
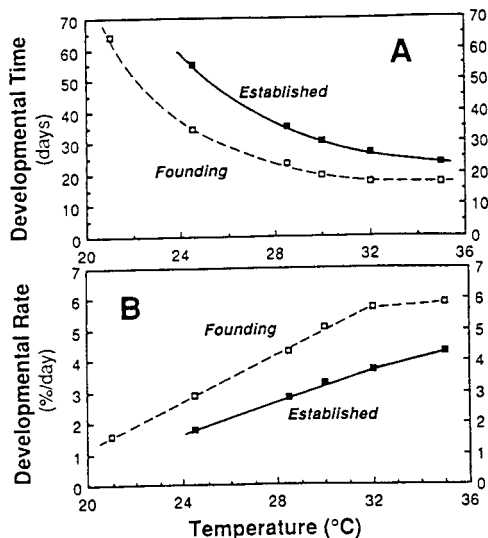
Fig. 2. (A) Total developmental times of worker brood from established colonies (see Fig. 1) and claustrally founding colonies. (B) Daily developmental rates as a percent of total developmental time ($100 \times 1/\text{total time}$) for the same colonies.

development times for first, second, and third instar larvae are 1, 2 and 2 days respectively. The time for fourth instar larvae was 6 days exclusive of the prepupal stage. Wheeler also reported that the duration of the fourth instar was extended an additional 4 days in larger individuals. I found that the durations of worker prepupae and yellow pupae were almost equal. Prepupae averaged 8.6 ± 0.4 (SE), 5.3 ± 0.7, 3.2 ± 0.3, 2.7 ± 0.2, 2.8 ± 0.2 and 1.8 ± 0 days for 21, 24.5, 28, 30, 32 and 35°C respectively. Pigmented pupae averaged 8.8 ± 0.1, 5.0 ± 0.1, 3.2 ± 0.1, 2.4 ± 0.2, 2.2 ± 0.1 and 1.9 ± 0.05 days for the same temperatures.

The developmental time for female sexual pupae was about $27 \pm 3\%$ longer than for worker pupae. Values for 28.5, 30, 32 and 35°C were, respectively: 13.2 ± 0.5 (SE), 11.3 ± 0.2, 9.7 ± 0.5 and 8.8 ± 0.9 days. Survival at 24.5°C was too low to make a comparison. Male pupae were not tested. O'Neal and Markin (1975a) published total developmental times of 35 days for sexuals and 28 days for major workers, both at 32°C. These values are probably fairly accurate, but their origin is puzzling because majors and sexuals are almost never produced in colonies as small as those they reportedly used (Porter and Tschinkel, 1985b; Wood and Tschinkel, 1981; O'Neal and Markin, 1975b).

Brood from founding colonies. Developmental times of miniature first generation workers (nanitics) produced by founding queens were $35 \pm 2\%$ shorter than times of minor workers produced in established colonies (Fig. 2A, 24.5–32°C). These results were similar to those reported by O'Neal and Markin (1975a), except at 35°C where they reported 26 days compared to 17 days in this paper (Fig. 2A). The difference might be attributed to their small sample size (5 queens) or possibly their queens were actually maintained at a slightly higher temperature which

may have retarded development. Banks *et al.* (1981) reported a total developmental time of 24–25 days at 28°C which is also very close to my observations (Fig. 2A).

Developmental times for egg, larval and pupal stages in founding colonies were less precise than values for brood from established colonies because founding colonies were inspected less frequently; nevertheless, results were consistent across temperature. Larvae of nanitics pupated in about half the time required for minor worker larvae. Egg and pupal stages were also shorter by about 25 and 10%, respectively.

Rates. Developmental rates in both foundling and established colonies increased almost linearly up to 32°C (Fig. 2B). Above 32°C, the rate of increase began to level off in founding colonies and probably mature colonies as well. Nanitic brood completed development at cooler temperatures than minor brood, but both terminated development when rates fell below 1.5% per day (Fig. 2B). Q_{10}s for both lines were almost the same, decreasing from around 4 at low temperatures to about 2 at higher ones. This decline is standard in most insects because developmental rates do not increase exponentially with temperature (Fig. 2B); a fact that makes the use of Q_{10}s with developmental data less than ideal (Powsner, 1935). Extrapolation to zero growth reveals theoretical growth threshold of about 17°C for both lines. Theoretical growth thresholds for minor worker eggs, larvae and pupae were 16.0, 17.5 and 17.5°C respectively. Thermal constants for production of nanitic and minor workers were respectively 259 ± 5 and 405 ± 7 degree-days (21.5–32°C).

Colony growth

Colony growth in *S. invicta* was highly temperature dependent (Fig. 3). Post-founding colonies grew successfully between 24 and 36°C with maximal rates at about 32°C. The pattern of production after 2 months was essentially the same for both large and small colonies (Fig. 3). All means for large colonies
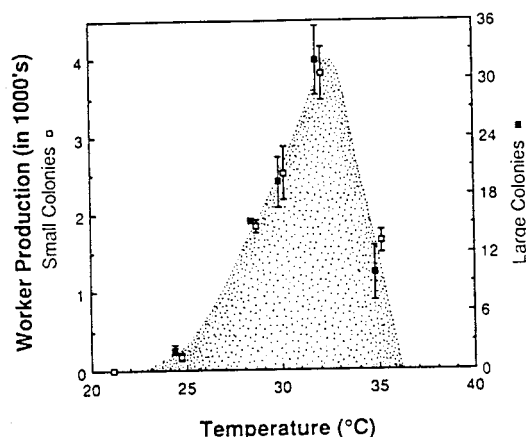

Fig. 3. Effect of temperature on net worker production in the fire ant, *Solenopsis invicta*. Worker production ($\pm$ SE) in large colonies (four replicates per mean) and small colonies (7–8 replicates) after 2 months. Note that large and small colonies use different scales on the y-axis.

were significantly different except for those at 28.5 and 30°C (Duncan's new multiple range test, $P < 0.05$; one-way ANOVA, data were log-transformed to equalize variance). Statistical results for small colonies were similar except that 28.5, 30 and 35°C means were not significantly different. Small colonies grew more rapidly on a percentage basis—a phenomenon commonly observed in social insects. Results for 1 and 2 months were similar. Net worker production (Fig. 3) does not include worker mortality; inclusion of dead individuals would have increased production values by 1–6% in the small colonies and about 10% in the larger colonies (24–32°C). Worker mortality at 35°C was much higher, small colonies averaged 18% and the larger ones about 50%.

While colony growth increased with temperature, the ratio of brood to workers generally decreased. For instance, brood-to-worker ratios in the small colonies after 2 months were: 2.35, 1.71, 1.28 and 0.88 for the experimental temperatures between 28 and 35°C. Ratios at 24.5°C were only 1.60, probably because this temperature approaches the lower threshold for brood production. This pattern was consistent for both colony sizes and sample periods. A decreasing ratio with higher temperatures is partially a result of larger colony size at these temperatures, but it is also probable that a given number of workers can tend more brood at cooler temperatures because of slower developmental times. Increased brood to worker ratios may partially counterbalance slower developmental times, but apparently not enough to have much effect on actual growth rates (Fig. 3).

DISCUSSION

Development

As expected, increasing temperature substantially reduced development times (Figs 1 and 2A). The effect of temperature on developmental rates of *S. invicta* (Fig. 2B) was essentially linear. Brood production ceased well above the temperature range where lower inhibition might occur (Wagner et al., 1984). Upper inhibition of developmental rates did occur (Fig. 2B), but *S. invicta* colonies almost always avoid temperatures in this range (>32°C; unpublished data; Cokendolpher and Francke, 1985). Consequently, simple degree-day procedures should be particularly applicable for modeling fire ant development. Some development does occur as low as 17°C, but developmental rates at cooler temperatures are so low that their contribution to overall growth would generally be minor.

Changing the temperature affected all three developmental stages uniformly (Fig. 1); in other words, the proportion of total developmental time required by each stage was independent of temperature. From a practical point of view, this means that developmental times in fire ants can be accurately predicted from partial data without measuring every stage at every temperature. For instance, the duration of larval instars can probably be predicted fairly accurately for different temperatures using Wheeler's developmental times (see Results) of larval instars at

30°C and the effect of temperature on total developmental time (Fig. 1). Similar calculations can also be made for sexual brood using O'Neal and Markin's (1975a) datum at 32°C. The proportion of time required for each developmental stage in other insects is also frequently independent of temperature, at least in the broad mid-range of the developmental curve (e.g. Powsner, 1935; also see references in Wagner et al., 1984).

Total development time in *S. invicta* varied considerably with different types of individuals. Generally, the larger the individual, the longer the development time. For instance, miniature nanitic brood (0.33 mg) required about 17 days to develop at 32°C (Fig. 2) compared to 26 days for minor worker brood (0.64 mg) and about 35 days for sexual brood (13.6 mg; O'Neal and Markin, 1975a). The theoretical minimal temperature for development (17°C, Fig. 2B), however, remained almost constant for all types of brood. The line connecting developmental rates simply rotated up or down about this theoretical minimum (Fig. 2B).

Overall, developmental times of nanitic workers were about 35% shorter than developmental times for minor workers in established colonies (Fig. 2). This shorter developmental time was principally due to faster larval development. Faster larval development probably resulted from the small size of nanitic workers; however, higher metabolic rates and better food quality may also have contributed. Faster development of nanitics was not limited to the larval stage. Nanitic pupae developed about 10% faster and eggs laid by founding queens developed about 25% faster.

Percent developmental times in founding colonies also remained almost constant across a broad temperature range (21–32°C) at 25% for eggs, 35% for larvae, and 40% for pupae. By comparison, equivalent proportions for minor worker brood in established colonies were: 21, 49 and 30%, respectively (24–32°C; Fig. 1). These values are almost identical to those reported by Wheeler (1982) for major workers of the ant *Pheidole bicarinata*. Minors of this species were similar, but required slightly less total time as larvae (23, 44, 33%). Corresponding percentages for pharaoh's ant eggs, larvae and pupae are 13, 60 and 27%, respectively (Peacock and Baxter, 1950). Equivalent values for honey-bee workers are 14, 46 and 40% (Jay, 1963).

Developmental times for *S. invicta* minor workers (Fig. 1) were quite similar to those reported for other social insects (Table 1). In fact, rates for most species were within 5–15% of rates observed for *S. invicta*. This is rather surprising considering the phylogenetic diversity and size differences of the organisms involved. Whatever the cause, it appears that intraspecific variation (Fig. 2, Table 1) often exceeds differences between species. Several species, however, have developmental rates considerably different from fire ants. For instance, honey-bee queens develop much faster than fire ant queens. Also, some solitary bees appear to have rather rapid development at room temperature (Torchio, 1984; Torchio, person. commun.).

Social Hymenoptera reputedly have unusually high developmental rates (Sehnal, 1985); however, a brief survey of the literature (see references in Wagner et

Table 1. Comparison of developmental rates of ants and other social Hymenoptera with developmental rates observed for minor workers of the fire ant, *Solenopsis invicta* (see Fig. 1)

Taxon and source	Temperature (°C)	Brood stage*	Duration (days)	S. invicta Duration	S. invicta (% Difference)
Ants					
Monomorium pharaonis	27†	E + L + P	38–45	41	(+1)
Peacock and Baxter, 1950					
Pheidole bicarinata (minor)	27	E + L + P	35	41	(−15)
Wheeler, 1982 (major)	27	E + L + P	40	41	(−2)
Myrmica rubra	25	L	24‡	25	(−4)
Weir, 1959					
M. rubra	25	PP	5.5§	5.1	(+8)
Myrmica ruginodis	25	PP	4.0§	5.1	(−22)
Myrmica sabuleti	25	PP	6.7§	5.1	(+31)
Myrmica scabrinodis	25	PP	6.0§	5.1	(+18)
Elmes and Wardlaw, 1983					
Iridomyrmex humilis	27	E + L + P	~44	41	(+7)
Newell, 1909					
Oecophylla longinoda	24–25	E + L + P	39	55	(−29)
Ledoux, 1950	27–30	E + L + P	28.5	37	(−23)
Formica rufa	26–30	E + L + P	35–37¶	35	(+3)
Otto, 1962					
Bees					
Apis mellifera (workers)	35	E + L + P	21	23	(−9)
Jay, 1963 (queens)	35	E + L + P	17	31**	(−45)
Wasps					
Polistes foederatus	25	L + P	40	40	(0)
Turillazzi and Conte, 1981					

*E: egg, L: larva, P: pupa, PP: prepupae; †Peacock and Baxter, 1949; ‡assuming first instars were 2 days old; §development only inspected weekly; ¶composite of several temperatures, 28°C was used as a mean. **Rate for fire ant queen estimated from O'Neal and Markin, 1975a and Fig. 1.

al., 1984) suggest that these rates are about average or even a little low compared to non-social insects at equivalent temperatures. In other words, short developmental periods in social Hymenoptera are probably more a function of high nest temperatures resulting from thermoregulation, rather than high developmental rates *per se*.

Colony growth

The temperature-growth curve for *S. invicta* colonies has a typical asymmetrical shape (Fig. 3), similar to developmental curves in other insects (Wagner *et al.*, 1984). The window of growth for established colonies spanned about 12°C (24–36°C, Fig. 3). Maximal rates of growth occurred at 32°C, which is very near the preferred temperature of 30–32°C for brood in intact laboratory colonies (unpublished observation, but note that this is 2–4°C higher than the preferred temperature reported by Cokendolpher and Francke (1985) for small groups of workers and brood). The rise of the growth curve between 24 and 32°C resulted from increasing metabolic rates and the fact that colonies at cool temperatures passed through fewer developmental periods during the 2-month test period (e.g. 1.1 at 24.5°C vs 2.2 at 32°C). Growth dropped off dramatically above 32°C. This decline apparently was not due to increased developmental times (Fig. 1) nor to increased pupal mortality, although cumulative detrimental effects are possible. High worker mortality was a contributing factor, but thermal stress may have impaired other functions such as oviposition, brood care, or food flow in the colony. The lower growth threshold of 24°C (Fig. 3) is curiously well above the theoretical minimum of 17°C. Exactly why successful production appears to terminate below about 1.5%

per day in both established and founding colonies (Fig. 2B) is unknown. Another phenomenon deserving further study is the possibility that larger individuals require higher minimum temperatures for successful development. The data is sketchy, but it appears that the growth window for nanitic workers is shifted several degrees toward cooler temperatures. Similarly the growth window for sexuals may be shifted toward warmer temperatures. Passera (1974) reported similar results for major and minor *Pheidole* workers.

Temperatures for maximal growth and the upper limit of growth (Fig. 3) are within the normal range for insects generally (see references in Wagner *et al.*, 1984). However, the lower limit of growth (Fig. 3) is unusually high in *S. invicta*. Most insects appear capable of completing development at 15°C or less with theoretical minima of 10–12°C (see Wagner *et al.*, 1984), whereas established *S. invicta* colonies cease growth below 24°C. This lower limit is partially due to poor survivorship of eggs and young larvae (Fig. 1), but the queen may cease oviposition at these cooler temperatures as well. Other species of ants also cease growth at fairly warm minimal temperatures. The lower limit for the production of *Pheidole* minors and majors are approx. 21 and 24°C, respectively (Passera, 1974). Newell (1909) reports that Argentine ant queens cease oviposition below 20°C. Similarly, *Formica rufa* queens are apparently unable to lay worker-producing eggs below 20°C (Otto, 1962). In other words, most ants seem to require relatively warm temperatures for successful colony growth. The high minimal thresholds and narrow growth window observed in *S. invicta* may also be positively correlated with its thermoregulatory capabilities. Honeybees, for instance, have a very narrow window of

normal growth (about 32–36°C) and a high minimal temperature (Seeley and Heinrich, 1981). Climate may also affect growth temperatures but the significance of this factor is yet to be determined. For example, ants in the genus *Myrmica* appear adapted for growth in cool climates. Optimal temperatures for four species in England are around 22°C with upper limits of about 28°C and lower limits somewhere around 16°C (Elmes and Wardlaw, 1983). These authors also report that those species inhabiting cooler habitats had higher developmental rates.

Nanitic workers are known to benefit founding colonies by allowing a queen to rear more workers from her limited energy reserves (Porter and Tschinkel, 1986). It appears that faster developmental rates may be another important evolutionary benefit for colony founding. Faster developmental times allow founding fire ant queens to rear their first worker generation about 1–3 weeks faster than they could with normal minor workers. This allows founding colonies a "headstart" in producing the second worker generation, especially important where brood raiding is a threat (Tschinkel, 1987). Another benefit is that nanitic brood can complete development at cooler temperatures, a decided advantage since soil temperatures in the spring are often rather cool and founding queens cannot thermoregulate as effectively as established colonies.

This study has quantified the general effects of temperature on fire ant brood development and colony growth. This information will provide a foundation for evaluating fire ant thermoregulation and modeling colony population dynamics. These results, however, are only an initial step toward understanding the effects of temperature on colony growth. Future studies should investigate the overall survivorship of brood at different temperatures, preferably in intact colonies. Unfortunately, this will be difficult because marking eggs or small larvae so that they can be detected upon pupation is not easy. The duration of larval development also needs further study because rates are probably more variable than the data suggest (Fig. 1). Higher feeding rates, dietary changes, the presence of a queen, or periods of starvation might accelerate or decelerate larval development. Colony growth was only monitored for 2 months in this investigation. Longer periods might provide different results especially in larger colonies where worker mortality and natality were similar. Longer time periods, however, may not be entirely realistic because field colonies generally experience high temperatures only during daylight hours for part of the year.

Effects of fluctuating temperatures (Ratte, 1985) also need to be studied because temperatures experienced in nature vary substantially from day to day, and even hour to hour. Colony growth should also be examined in thermal gradients because different castes and developmental stages in field colonies may simultaneously select different temperatures in the soil column (Ceusters, 1977). For example, eggs might survive better at cooler temperatures than pupae; if so, colonies may grow best in a temperature gradient, rather than a single constant temperature. Short-term acclimation, seasonal brood cycles, and facultative control of developmental rates should also

be investigated. In conclusion, a great deal of specific work remains to be done concerning the effects of temperature on the growth and development of fire ant colonies.

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